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Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence

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One of the most apparent examples of cooperation between unrelated individuals is biparental care whereby the male and the female parent share the rearing of the offspring. Theoretical models of care predict that selection should favour biparental care if it substantially improves the survival of the offspring. Although various ecological factors have been proposed to necessitate biparental care, experimental evidence is scant given the challenges of manipulating ecological factors in the natural habitat of animals. We carried out one such experiment in a small shorebird, the Kentish plover *Charadrius alexandrinus*, that breeds in an extreme desert environment. Nest cover and thus exposure to solar radiation vary between nests, and we show that parents at exposed nests spend more time incubating than those at nests shaded by a bush (covered nests). Experimental removal and supplementation of nest cover gave results consistent with the observational data; at experimentally exposed nests both males and females increased incubation effort and they changed over incubation more frequently, whereas at experimentally covered nests we observed the opposite. We conclude that exposure to extreme solar radiation influences biparental care and necessitate parental cooperation in the Kentish plover. Furthermore, since parental care often co-evolves with mating strategies, we conjecture that where the environment puts less pressure on the parents and provides the opportunity for reduced care, both mating systems and parental care can diversify over evolutionary time.

Biparental care, i. e., provisioning of the young by both the male and female parents, is a prominent example of cooperation and conflict in social behaviour of animals and humans (Alexander 1974; Maynard Smith 1982; McNamara and Weissing 2010). By cooperating, the parents improve the survival of their offspring, whereas by withholding care they may preserve their resources to survive and breed later in life (Trivers 1972; Houston et al. 2005; Kvarnemo 2010). Animals have adopted various solutions to balance the conflict and cooperation, as evidenced by the diverse parental behaviours exhibited by a variety of insects, fishes, frogs, birds and mammals (Clutton-Brock 1991; Duellman 1992; Tallamy 2001; Reynolds et al. 2002; McGraw et al. 2010). Theoretical models of parental care consistently predict that if care by two parents improves the survival of the young substantially more than by a single parent, biparental care is expected (reviewed by Clutton-Brock 1991; Székely et al. 1996; Houston et al. 2005; Kvarnemo 2010), assuming phylogenetically and physiologically flexible behaviours.

The ecological and social factors influencing the evolution of parental care have been the subject of contention for decades (Trivers 1972; Wilson 1975; Maynard Smith 1982), and debates concerning this issue continue (Kvarnemo 2010; Jennions & Kokko 2010; McGraw et al. 2010). One long-standing hypothesis posits that parents should jointly rear their young (biparental care, a form of parental cooperation defined here as behavioural actions by a male and a female that target improving offspring survival) in an environment that is hostile for the developing young (Lack 1968; Wilson 1975; Jones et al. 2002; Carey 2002). Extreme weather conditions, food scarcity, intense competition between neighbours, desiccation of eggs and high predation of the offspring may select for enhanced biparental care (Wynne-Edwards 1998; Amat et al. 1999; Kosztolányi et al. 2006; Tieleman et al. 2008; Brown et al. 2010).

Testing the harsh environment hypothesis, however, is challenging for two reasons. First, it has proven difficult to identify specific ecological factors that select for biparental care in natural populations. Ecological factors tend to act in concert, and teasing apart which are the key elements require long-term data on both ecology and parental behaviour. Second, experimentally altering the hypothesized component of the environment to induce changes in parental behaviour is often

64 extremely difficult, and previous studies were therefore observational or carried out in the laboratory,
65 except a recent study by Brown et al. (2010) that used a combination of phylogenetic analyses and
66 field experiments in tropical frogs to test whether biparental care is influenced by pool size of the
67 developing tadpoles.

68 Here we test the harsh environment hypothesis by experimentally manipulating nest cover in a
69 small ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*. Nest environment has
70 been experimentally investigated previously (Martin & Ghalambor 1999; Reid et al. 2000; Cresswell
71 et al. 2004; Amat & Masero 2004a; Kim & Monaghan 2005; D'Alba et al. 2009), although our
72 experiment is novel because we are focusing on the behaviour of both parents and thus are interested
73 in cooperation behaviour, whereas the aforementioned experiments investigated the responses of a
74 single parent, usually the female, since only one parent incubates or the authors were not able to
75 distinguish the sexes. The distinction between single-parent and biparental systems is important,
76 because the theoretical frameworks for the responses are fundamentally different; game-theoretic
77 *versus* non-game-theoretic approach. Furthermore, experimental studies showed that the joint
78 response of both parents is often different from individual responses; for instance handicapping one
79 parent in biparental species found diverse joint responses by the pair, since the manipulated parent's
80 mate reduced, increased or maintained their level of care (Harrison et al. 2009).

81 The Kentish plover is an ideal species to test the harsh environment hypothesis, since it breeds
82 in deserts where ground temperatures may exceed 60 °C (Amat & Masero 2004a; AlRashidi et al.
83 2010). Both parents incubate the eggs, although incubation behaviour varies between populations
84 (Vincze, O., C. Küpper, A. Kosztolányi, M. AlRashidi & T. Székely unpublished data). The parents
85 exhibit flexible behaviour: they carefully adjust their own incubation in response to their mate's
86 behaviour (Kosztolányi et al. 2009). The eggs are laid on the ground, so both the eggs and the
87 incubating adults are directly exposed to the ambient environment. Finally, some nests are under
88 bushes and thus the eggs are protected from direct solar radiation, whereas others are in the open and
89 thus fully exposed to it. This behavioural flexibility and natural variation in nest sites provide
90 excellent opportunities to test the responses of parents to experimental manipulation of the ambient

environment. Due to its amenability to experimental manipulations and its wide geographic range, the Kentish plover is becoming an avian model species to understand conflict and cooperation in the context of breeding system evolution (Lessells 1984; Amat & Masero 2004a; Kosztolányi et al. 2006; Székely et al. 2007; AlRashidi et al. 2010). Males tend to incubate during the night whereas females do most of the daylight incubation (Fraga & Amat 1996; Kosztolányi & Székely 2002), however, there is substantial variation in incubation behaviour between populations especially at midday (Amat & Masero 2004a, AlRashidi et al. 2010). Some of this variation appears to be related ambient temperature since in hot locations the nests are almost constantly covered in mid-day (AlRashidi et al. 2010), and the parents appear to struggle incubating long stints presumably due to the risk of overheating (Amat & Masero 2004b).

The current study has two objectives. First, we compared the level of biparental care between naturally exposed and covered nests. We predicted that parents nesting at exposed sites will exhibit more biparental care. In addition, they will have more frequent nest changeovers especially during the hottest part of the day (AlRashidi et al. 2010). Second, we manipulated the environment of the nests by either covering or exposing them. We predicted that at experimentally exposed nests the parents will increase their incubation effort and make more frequent nest changeovers, whereas at experimentally covered nests we expected the opposite.

METHODS

Study Site and General Field Procedures

Fieldwork was carried out in two years (17 April - 4 July 2008, 15 May – 4 July 2009) in Farasan Island in the Red Sea (Kingdom of Saudi Arabia, 16° 48' N 41° 53' E) over a period that coincided with peak breeding activity of Kentish plovers. Farasan Island has a subtropical desert climate and the average annual precipitation is less than 50 mm (NCWCD 2000). Halophytic plants (*Halopeplis perfoliata, Zygophyllum album, Zygophyllum coccineum, Zygophyllum simplex,*

116 *Limonium axillare*, *Suaeda monoica*) cover large areas of salt marsh and sand dunes, providing
117 nesting sites for plovers (NCWCD 2000).

118 Kentish plovers breed up to 1 km away from the seashore. For each nest we recorded clutch
119 size, photographed the nest and determined its geographic (UTM) coordinates using a hand held GPS
120 unit. Nests were allocated to five categories: exposed nests that had no vegetation cover (0), < 25%
121 cover (1), 25-50% cover (2), 51-75% cover (3) and >75% cover (4). We checked the repeatability of
122 nest cover classification (Harper 1994): one observer (MAR) scored cover in the field and took
123 photographs, and two observers (AK, CK) re-scored these photographs twice blindly to nest ID. Nest-
124 cover scores were highly repeatable between the three observers (r = 0.939, $F_{31,64}$= 47.837, P< 0.001).
125 Date of egg-laying was estimated by floating the eggs in lukewarm water (Székely et al. 2008). The
126 sea was the only water source for the birds, and UTM coordinates were used to estimate the
127 perpendicular distance between the nest and the nearest coastline.

128

129 *Recording Incubation Behaviour and Ambient Temperature*

130 Both parents were captured on the nest on the same day or on subsequent days using funnel
131 traps, and they were marked with 1-3 colour rings and one metal ring provided by Saudi Wildlife
132 Commission. All breeding birds were individually ringed, no individual was included more than once
133 in the two-year data set. Adults have sexually dimorphic plumage (Fig 1): males have black eye-
134 stripes, frontal bars and breast-bands, whereas females are drab (Cramp & Simmons 1983). Behaviour
135 was only recorded at nests category 0 (which we shall term 'exposed nests'), or at 3 and 4 ('covered
136 nests'). Incubation data were collected at 32 nests (17 and 15 covered and exposed nests,
137 respectively).

138 Incubation was recorded by either a Trovan Flex™ Transponder, LID665 decoder (Dorset
139 identification B.V., Aalten, Netherlands), or by using a digital video camera (Sony Handycam
140 HC44E, Sony Corporation, Japan). The transponder system consisted of a small chip (approx 0.4 g; ≈

1 % of adult body mass) with unique identification code which was glued on the tail of each parent. The antenna of the transponder decoder was buried approximately 3-5 cm under the nest, and connected to a data logger. The system recorded every 20s whether each parent was on the nest for at least 24h (n = 27 nests).

The video camera was used to record the incubation behaviour at five nests in 2008. The camera was positioned about 1 m from the nest, and it recorded an image every 20s and was changed manually to night-shot mode for night-time images. The camera was covered by a small cardboard and some vegetation, and all other parts of the system (including the battery) were buried under the ground. The installation of the transponder and camera systems (15-20min) was carried out early in the morning, or late afternoon to avoid heat stress. The parents returned to the nest after a few minutes.

Ambient ground temperature was measured at all nests (n = 32 nests) by a thermo-probe which was placed about 25 cm from each nest scrape at ground level in an open, un-shaded area. The probe was connected to a data logger (Tinytag, Gemini Data Loggers Ltd.) that recorded the temperature every 20s for at least 24h. The minimum and maximum ground temperatures were 23.8 °C and 60.3 °C, respectively, during the study (Fig. 1 C). Sitting tight on the ground exposed to solar radiation is a major challenge for desert-nesting birds (Grant 1982). Amat and Masero (2004a) showed that the operative temperatures (the sum of radiative and convective factors) were 10-15 °C higher at exposed nests of Kentish plovers than at covered nests, and consistently, the incubating parents exhibited behaviours indicating heat stress (e.g. panting, belly-soaking; see Fig 1).

Nest Cover Manipulation

At 27 nests where the transponder system was used, we used a control period of 24h to estimate natural behaviour, then we experimentally manipulated nest cover for another 24h by completely removing cover from covered nests (‘cover-removed nests’), or by covering exposed nests with

166 bushes which shaded the nest ('cover-added nests', Fig.2). Data from 20 nests were used in the
167 analyses (11 covered nests and 9 exposed nests), because seven nests were predated before the trials
168 terminated (3 covered and 4 exposed nests). Parents took 1-107 min to return to the manipulated
169 nests. We gave parents at least 6h to adjust to the manipulation of their nest cover before we started to
170 record incubation behaviour. After 24h of recording, the transponder system was removed and nests
171 were returned to their natural cover-type by returning the original bush to the covered nests, and
172 removing bushes from exposed nests.

173

174 *Data Analysis*

175 24-hour recordings were considered as the unit of analysis and each day was divided into
176 twelve two-hour time periods. Following AlRashidi et al. (2010) four behavioural variables were
177 calculated for each period: (1) total incubation, i.e. % of time when the eggs were incubated by either
178 parent; (2) male incubation, i.e. % of time when the eggs were incubated by the male, (3) female
179 incubation, i.e. % of time when the clutch was incubated by the female, (4) number of changeovers,
180 i.e. the number of events when one parent was relieved by the other parent. The average ground
181 temperature outside the nests was taken as the ambient temperature for each period.

182 The influence of natural nest cover on incubation behaviour (response variable) was
183 investigated using linear mixed-effects models (Pinheiro& Bates 2000). Nest identity was included as
184 a random factor, since parental behaviour is not independent between two-hour time periods for a
185 given nest. The following fixed effects were included in the initial models: nest cover (factor with two
186 levels: exposed or covered), time period (factor), sea distance (covariate), year (factor), egg laying
187 date (covariate, given as no. of days since 1 March), age of clutch in days (covariate). Conway and
188 Martin (2000) found that incubation behaviour and ambient temperature are not linearly associated,
189 thus ambient temperature was included in the models as second degree orthogonal polynomial
190 covariate. The effect of temperature on incubation may vary over the day (AlRashidi et al. 2010), and
191 therefore the interaction between time period and ambient temperature was also included in initial

models. In the initial models of male and female incubation, incubation by the other sex was also included as fixed term because in shared incubation systems the behaviour of a parent is influenced by the behaviour of its mate (Kosztolányi et al. 2009). Furthermore, nest cover type × time period interaction was included in all initial models to test whether cover type may have different effect depending on the time of the day.

Experimental data were also investigated using linear mixed-effects models. We used the difference in incubation behaviour after manipulation minus before manipulation for the behavioural variables (1-4 variables as defined above) as response variables. Initial models included nest identity as a random factor, treatment (with two levels: cover-added and cover-removed), time period and period × treatment interaction as fixed terms. Each nest served as its own control, therefore confounding variables (see above) were not included in models of experimental data. In the initial models of male and female incubation, the incubation by the other sex was also included as fixed covariate (see rationale above).

Percentage variables (converted to proportions) were arcsine square-root transformed, and number of changeovers was $ln(x + 1)$ transformed to normalize residual distributions. Initial models were fitted using maximum likelihood method. Model selection was carried out using the function stepAIC in MASS package. We report the final model refitted using Restricted Maximum Likelihood (REML). The amount of variance explained by the random effect was investigated by comparing the final model with a Generalized Least Squares (GLS) model containing the same variables as the final mixed-effects model. We used R version 2.10.0 for statistical analyses (R Development Core team 2010). Values are given as mean ± SE unless stated otherwise.

The distribution of nest types (covered and exposed) was not different between the two years of the study (Fisher's exact test, $P = 0.444$). Neither body mass, nor wing length and tarsus length were different between nest cover categories in males or females (MANOVAs, $P \geq 0.190$). Finally, average ambient temperature, egg-laying date, age of clutch and distance to sea were not different between nest types (t-tests, $P \geq 413$).

218

219 *Ethical Note*

220 Fieldwork and the nest cover manipulation were licensed by the Saudi Ministry of
221 Environment. We targeted a short-term manipulation using minimum sample sizes to minimise the
222 welfare impacts on the subjects. It is unlikely that our experiment substantially influenced the parents'
223 survival or their reproductive success, since the manipulations were within the natural range of nest
224 cover. Manipulation was carried out early in the morning (five nests) (i.e. between 06:00 and 10:00),
225 or late afternoon (15 nests) (i.e. between 17:00 and 20:00) to reduce the risk of heat stress. Nest
226 predation by white-tailed mongoose (*Ichneumia albicauda*) and stray cats were very high in our study
227 site: 80.1% of the clutches were predated whereas only 14.8% of clutches produced at least one chick
228 (n = 196 nests). Daily survival of experimental nests was 0.87 (95% Confidence Intervals: 0.78 -
229 0.96), and the confidence intervals include the daily survival of all nests in our study site (0.92, MAR
230 unpublished data). Finally, we did not find any indication that incubating plovers were predated on (or
231 near to) their nests (n = 272 nests, MAR unpublished data).

232

233 **RESULTS**

234 *Incubation at Naturally Exposed and Covered Nests*

235 Both males and females spent significantly more time on incubation at exposed nests than at covered
236 ones over the whole day, and biparental incubation was more extensive at exposed nests (Fig. 3,
237 Tables 1 & 2). The number of changeovers was also higher at exposed nests (Fig. 3, Tables 1 & 2). In
238 addition, both male and female incubation were influenced by time of day, and ambient temperature
239 (Table 2). Incubation behaviour of the mate declined with incubation behaviour of the focal parent
240 (Table 2, see also AlRashidi et al. 2010). Female incubation tended to be higher throughout the day,
241 whereas the males increased at night and reduced during mid-day (Fig. 3). Finally, total incubation,

242 female incubation, male incubation and number of changeovers all increased with the age of the
243 clutch (Table 2).

244

245 *Incubation at Experimentally Manipulated Nests*

246 Manipulation of nest cover influenced parental behaviour in all response variables (Fig. 4, Table 3).
247 After manipulation, parents at cover-added nests reduced incubation efforts, whereas parents at cover-
248 removed nests increased their incubation. Therefore, the level of biparental incubation increased at
249 cover-removed nests, and decreased at cover-added nests (Fig. 4). As expected, at cover-removed
250 nests the number of changeovers increased whereas at cover-added it decreased (Table 3), and the
251 effects were the largest during the hottest part of the day (Fig. 4). Consistent with the results at
252 unmanipulated nests, the behaviour of mate also influenced both male and female incubation at
253 experimentally manipulated nests (Table 3).

254

255 **DISCUSSION**

256 The ecological and social factors influencing the evolution of biparental care is debated (Kvarnemo
257 2010; Jennions & Kokko 2010; McGraw et al. 2010), although progress has been made in some taxa
258 (Thomas & Székely 2005; Gonzalez-Voyer et al. 2008; Brown et al. 2010). Here we show that
259 exposure to solar radiation evokes more parental effort and thus necessitates a higher level of
260 biparental care especially during mid-day when the nests are exposed to intense solar radiation. Both
261 observational and experimental data consistently show that nest cover and exposure to solar radiation
262 significantly influence incubation behaviour of both males and females. The increased total incubation
263 and changeovers at exposed nests are likely to reduce the risk of overheating to the eggs and to the
264 parents themselves (Amat & Masero 2004a). By relieving each other frequently from incubation
265 duties parents can fly to the sea, and wet their ventral plumage (i. e. belly-soaking), so that they can
266 cool their eggs and themselves (Grant 1982; Amat & Masero 2009). Note that our results are not

directly comparable to the non-experimental study of AlRashidi et al. (2010), since nest cover likely to change the thermal conditions at the nest over the full day, and this effect may interact with the time periods and ambient temperature.

The diurnal pattern in behavioural responses, however, was different for total incubation and nest changeovers. At cover-removed nests changeovers were especially frequent in the hottest part of the day (between 10.00 and 16.00), whereas total incubation during the same period was hardly different from the control. We believe this is due to a ceiling effect: in the middle of the day all nests are covered practically all the time (AlRashidi et al. 2010), although by increasing the frequency of changeovers at cover-removed nests the parents can reduce the risk of overheating themselves. The latter result also suggests that parents carefully monitor their mate's behaviour, and alter their own care effort to compensate if necessary, consistent with an experimental manipulation of parental workload (Kosztolányi et al. 2009).

Interestingly, the diurnal contribution of males at exposed nests was less than at covered nests; possibly because males of exposed nests spent more time incubating the clutch at night. We suggest two explanations for the higher nocturnal nest attendance of males (and higher total incubation) at exposed nests. First, an exposed nest may be safer for the incubating parent than a covered nest (Grant 1982; Martin & Roper 1988; Amat & Masero 2004b), since exposed nests may facilitate the detection of predators at night allowing the parents to incubate for long periods. It also facilitates early escape if a predator approaches the nest. Second, nocturnal heat dissipation may differ between covered and exposed nests. Open nests may lose more heat at night than covered nests, and thus incubating parents should spend more time covering the eggs at night in the open. Consequently, in a desert environment nest cover by bushes appears to create a thermally favourable condition, although it might imply higher risks for the nest and/or the incubating adults. Both of these propositions require further field studies and we suggest that local adjustments in one (or both) of these components may explain differences between studies in behaviour of parents (Purdue 1976; Amat & Masero 2004a; AlRashidi et al. 2010; this study).

294 *Biparental Care and Harsh Environment*

295 Our study is one of the few experimental studies that showed environmental harshness
296 promotes biparental care. Brown et al. (2010) found biparental care was essential to tadpole survival
297 in small (but not large) breeding pools in frogs, because small pools had insufficient nutrients for
298 tadpole growth and survival. In the biparental California mouse *Peromyscus californicus* male
299 presence improved pup survival and shortened female interbirth interval, although the effects were
300 only apparent when food was limited (Cantoni & Brown 1997). In the dwarf hamster *Phodopus*
301 *campbelli* that breeds in an extremely cold environment where ambient temperatures may reach below
302 -30°C, care by both parents was critical to protect pups and parents from hostile weather (Wynne-
303 Edwards 1998).

304 Biparental care is exhibited by several phylogenetically distinct taxa living in different climate
305 conditions; we need further experimental and comparative analyses to understand this trait (Clutton-
306 Brock 1991; Duellman 1992; Reynolds et al. 2002; McGraw et al. 2010). Since the life-histories and
307 the precise nature of 'environmental harshness' may vary between populations, careful comparative
308 and experimental analyses are needed (Wilson 1975; Clutton-Brock 1991; McGraw et al. 2010). One
309 could argue that extreme cold (or hot) may not be 'harsh' for the organisms that are adapted to live in
310 these seemingly hostile environments, and the 'harsh' label may simply reflect a human-biased
311 perception of the animals' environment. However, the behavioural signs of stress and the carefully
312 tuned behaviours – for instance the ones we report here exhibited by nesting Kentish plovers –
313 suggest extreme habitats are challenging even for those organisms that are physiologically adapted to
314 breed there.

315 Further investigations of environmental harshness need to consider that environments are
316 complex, and different components may put opposing selection pressures favouring or disfavouring
317 parental cooperation (Kosztolányi et al. 2006; McGraw et al. 2010). For instance, Arctic breeding
318 birds have to cope with sub-zero ambient temperatures even during the short polar summer, and the
319 demands to incubate the eggs and brood the chicks are expected to promote biparental care. However,

using phylogenetic analyses García-Peña et al. (2009) showed uniparental care was more common in Arctic shorebirds than in temperate and tropical ones. They argued that Arctic environments provide exceptionally abundant food for both the chicks and the parents, and thus relax the pressure for biparental care. Therefore one parent can be emancipated from parental duties.

Biparental Care, Conflict and Diversification

Although pioneering works suggested that breeding strategies, including parental care, have far-reaching evolutionary implications (Trivers 1972; Emlen & Oring 1977), we are only beginning to realise how complex these interactions may be (Wilkinson & Birge 2010). Conflict between individuals, for instance sexual conflict, is often seen as an evolutionary process that drives phenotypic diversification and speciation (Queller & Strassman 2009). Sexual conflict and sexually antagonistic coevolution may produce diverse traits (Chapman et al. 2003, Arnqvist & Rowe 2005), whereby the conflicting interests between males and females lead to divergent traits between populations (Gavrilets & Waxman 2002). Therefore, a benign environment where the demand for biparental care is relaxed may facilitate rapid phenotypic evolution. Consistent with these arguments, more intense sexual selection and sexual conflict were associated with higher rates of phenotypic diversification (Thomas et al. 2006; Gonzalez-Voyer et al 2008).

We argue, however, that under certain situations, harsh environments and parental cooperation may also facilitate diversification. Firstly, in harsh environments males and females may keep the same partner throughout their life (mate-retention, Ens et al. 1996), and this likely to reduce gene-flow between breeding locations, and populations can adapt to their local environment unless gene-flow is counter-balanced by immigration or natal dispersal. In contrast, since short pair-bonds and promiscuity are often associated with mate-seeking behaviour and dispersal between populations, these would create a panmictic population that reduces the chance of the evolution of locally adaptive traits. Secondly, harsh environments may demand specific adaptations to live and breed successfully, and closely related organisms may invent different solutions to environmental challenges. For

instance frogs, which seem distinctly unsuited for a terrestrial existence, have adapted in extraordinary ways to life on land and invented over 30 reproductive strategies including direct development, eggs (or tadpole) transport by the parent, foam nests and biparental egg guarding (Duellman 1992, Wells 2007).

In conclusion, our results in a small shorebird that breeds in a desert environment suggest harsh environments influence a social trait, biparental behaviour, since nest exposure in association with extremely hot ambient temperature favoured parental cooperation. Increased parental cooperation appears to be important in a desert environment, since a single parent – as also argued by Amat & Masero (2004) - may not be able to protect the eggs and/or itself from overheating. Experimental analyses of male-female interactions, measuring the physiological responses of males and females to various manipulations, and comparing the incubation responses of males and females across different populations are needed to reveal the complex relationships between environmental factors and parental cooperation.

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492 **Table 1**: Incubation behaviour (mean ± SE) over 24 hours at Kentish plover nests (17 and 15 naturally
493 covered and exposed nests, respectively).

	Total incubation (%)	**Male incubation (%)**	**Female incubation (%)**	**Number of changeovers**
Covered	74.03 ± 3.04	39.89 ± 2.23	34.15 ± 2.60	15.00 ± 1.20
Exposed	81.69 ± 1.96	41.50 ± 2.56	40.20 ± 2.40	20.33 ± 1.77

1 **Table 2**: Minimal mixed-effects models of incubation behaviour in 32 Kentish plover nests with natural extent of exposure

Explanatory variables	**Response variable**											
	Total incubation (%)			**Male incubation (%)**			**Female incubation (%)**			**Number of changeovers**		
	df	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***
Cover type	1, 29	9.048	0.005	1, 29	5.777	0.023	1, 29	8.881	0.006	1, 27	6.209	0.019
Time period	11, 328	11.804	<0.001	11, 316	1.842	0.047	11, 327	14.389	<0.001	11, 317	2.578	0.004
Temperature	2, 328	10.713	<0.001	2, 316	5.146	0.007	2, 327	5.041	0.007	2, 317	0.038	0.920
Time period x temperature	-	-	-	22, 316	2.216	0.002	-	-	-	22, 317	2.071	0.004
Time period x Cover type	11,328	2.136	0.018	-	-	-	11,327	2.100	0.020	-	-	-
Female incubation	-	-	-	1, 316	244.260	<0.001	-	-	-	-	-	-
Male incubation	-	-	-	-	-	-	1, 327	291.187	<0.001	-	-	-
Age of clutch	1, 29	17.325	<0.001	1, 29	8.479	0.007	1, 29	16.004	<0.001	1, 27	4.089	0.053
Likelihood ratio test for the	$\chi^2 = 12.795$, $df = 1$, $P < 0.001$			$\chi^2 = 9.770$, $df = 1$, $P = 0.002$			$\chi^2 = 11.325$, $df = 1$, $P = 0.001$			$\chi^2 = 7.446$, $df = 1$, $P =$		

random effect	0.006

Note: Cover type refers to exposed or covered nests (see Methods), temperature was included as a second order polynomial, *df* values are numerator and denominator degrees of freedom, respectively. For the number of changeovers the final model also included the following terms: egg laying date: $F_{1,27} = 2.830$, $P = 0.104$, sea distance: $F_{1,27} = 4.961$, $P = 0.034$. The empty cells indicate that the variable was either eliminated during model selection, or it was not included in the initial model (see Methods for details). Dash indicates terms that were not included in the final models.

Table 3: Minimal mixed-effects models for experimentally manipulated Kentish plover nests (cover-added, cover-removed).

Explanatory variables	**Response variable**											
	Total incubation (%)			**Male incubation (%)**			**Female incubation (%)**			**Number of changeovers**		
	df	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***	***df***	***F***	***P***
Treatment	1, 18	7.66	0.013	1, 18	4.76	0.043	1, 18	9.39	0.007	1, 18	25.081	<0.001
Time period	-	-	-	-	-	-	-	-	-	11,198	1.183	0.301
Time period x Treatment	-	-	-	-	-	-	-	-	-	11,198	4.535	<0.001
Female incubation	-	-	-	1, 219	184.72	<0.001	-	-	-	-	-	-
Male incubation	-	-	-	-	-	-	1, 219	184.79	<0.001	-	-	-
Likelihood ratio test for the random effect	$\chi^2 = 6.826$, $df = 1$, $P = 0.009$			$\chi^2 = 8.804$, $df = 1$, $P = 0.003$			$\chi^2 = 4.165$, $df = 1$, $P = 0.041$			$\chi^2 < 0.001$, $df = 1$, $P = 1$		

Note: *df* values are numerator and denominator degrees of freedom, respectively. For legend see Table 2.

Figure legends

Figure 1. Kentish plover parents attending exposed nests, (a) male, (b) female. Note the crouched posture of parents and the wet belly-feathers. (c) Ambient temperature over the day (mean ± SE).

Figure 2. Examples of nest cover manipulations: before and after manipulation at different nests.

Figure 3. Incubation behaviour at naturally covered and exposed Kentish plover nests (17 and 15 nests, respectively). (a) Total incubation (mean ± SE), (b) number of changeovers, (c) male incubation and (d) female incubation.

Figure 4. Incubation behaviour at experimentally manipulated Kentish plover nests**:** cover-removed nests (n = 11) and cover-added nests (n = 9). (a) Change in total incubation (mean ± SE). (b) Change in number of changeovers.

Figure

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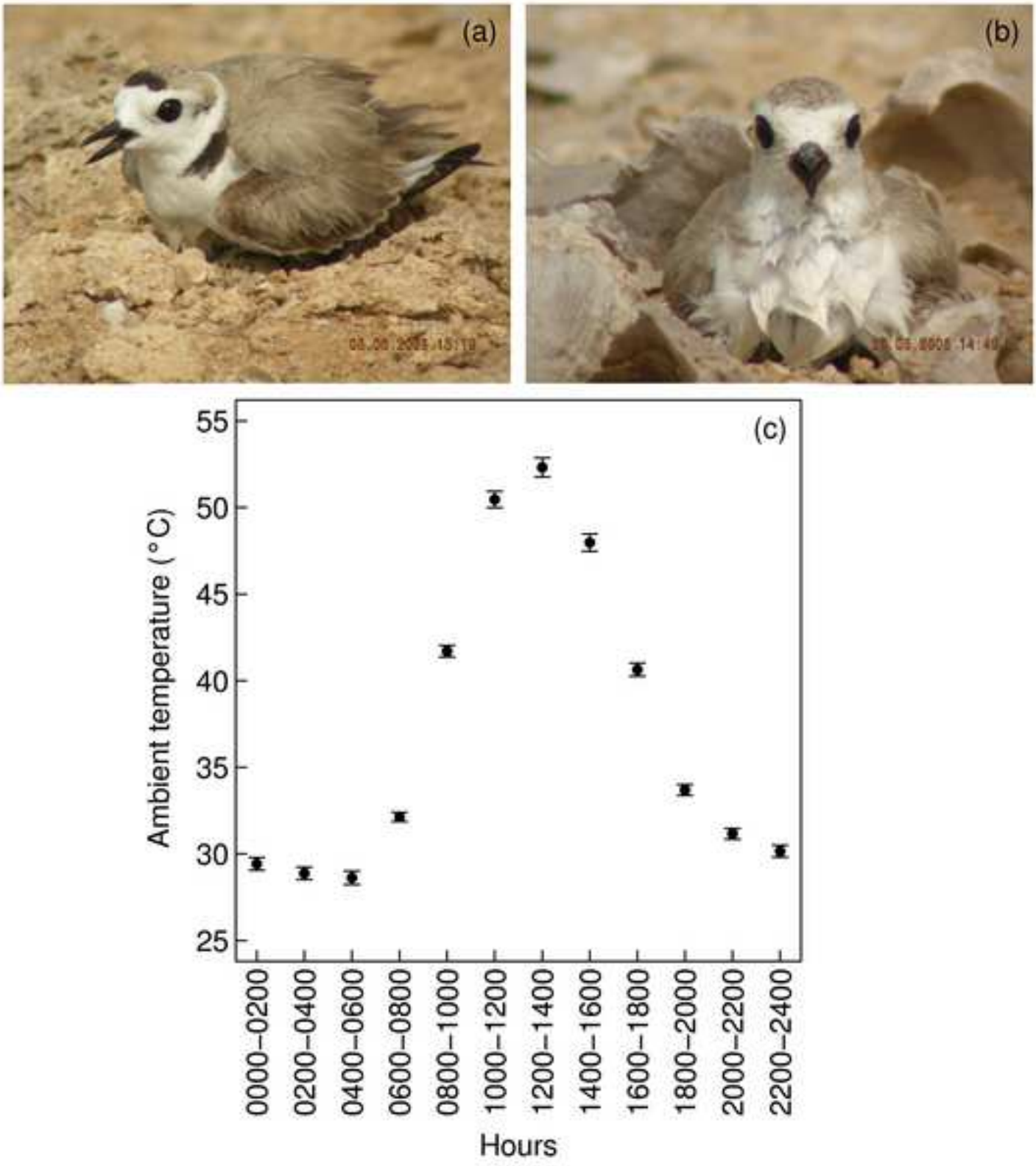

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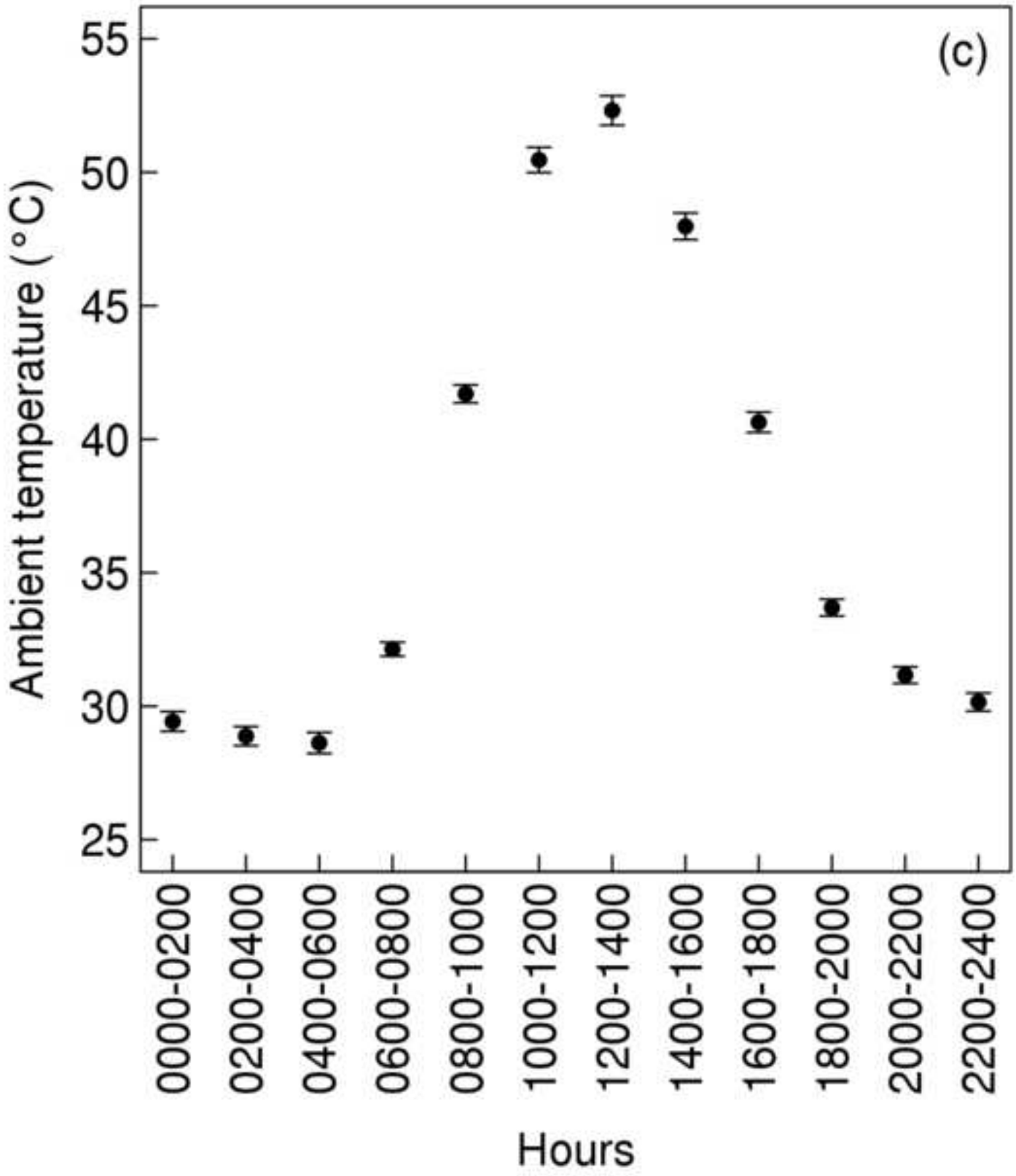

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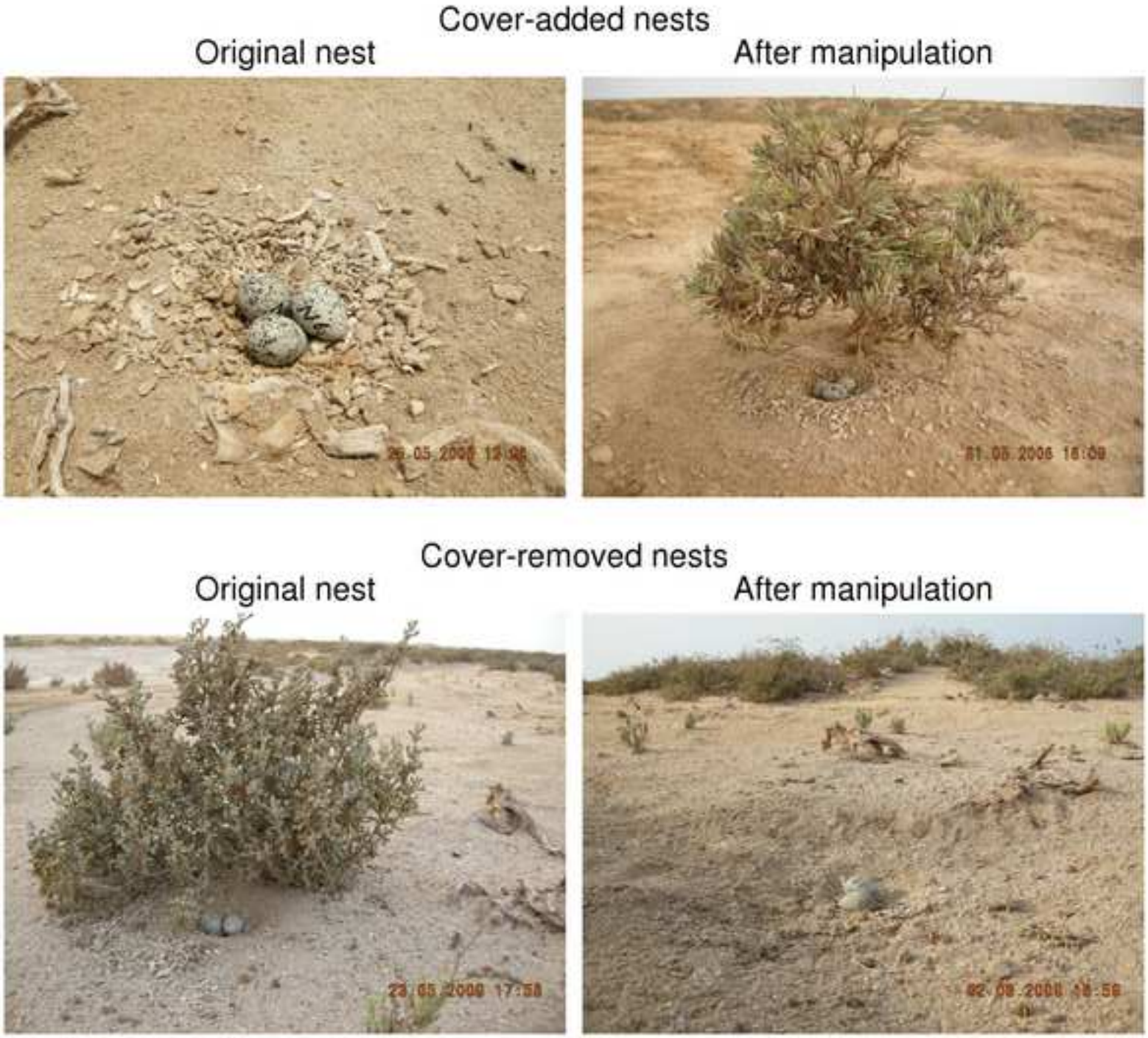

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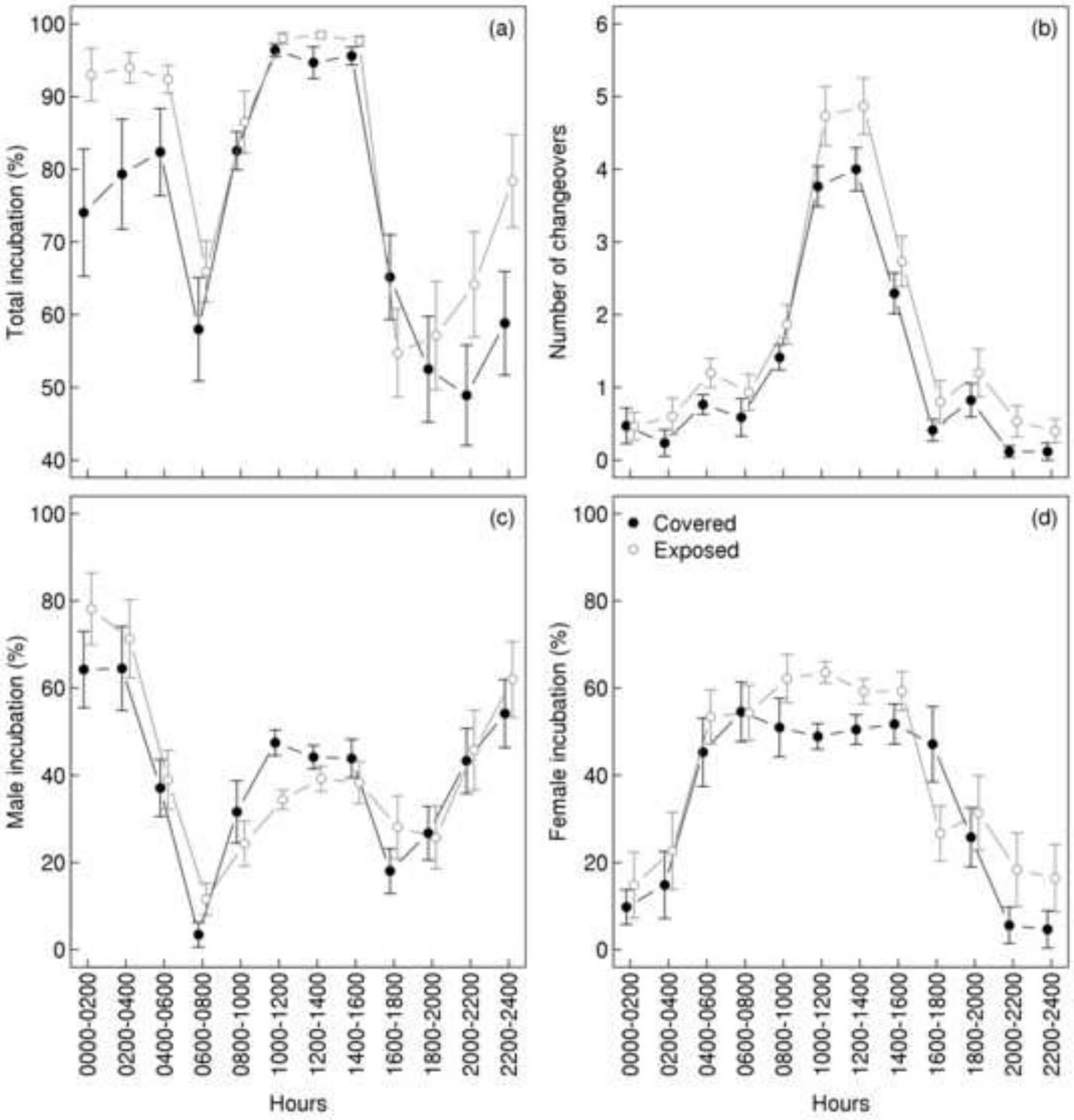

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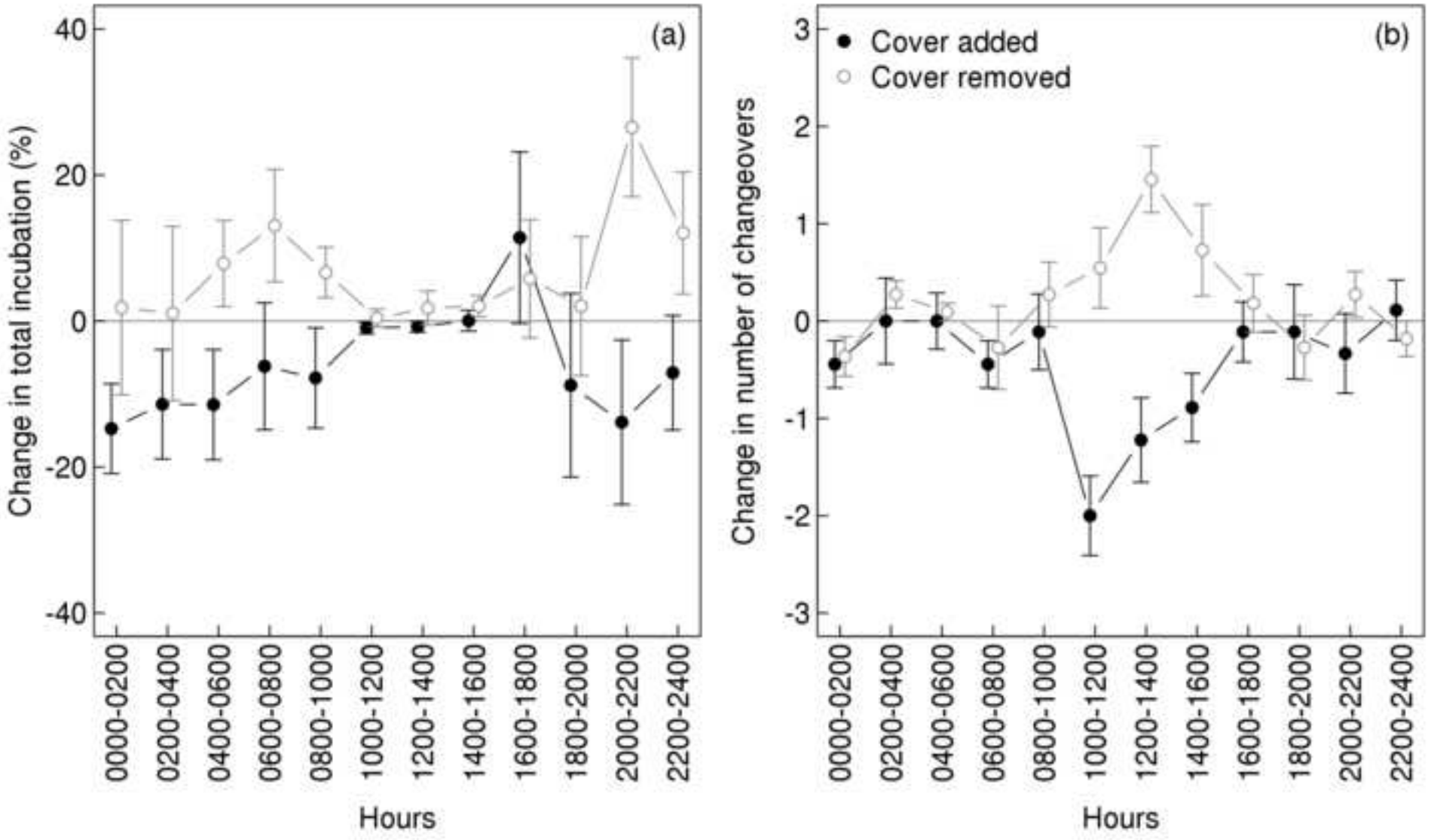
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